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OBSERVATIONS ON THE SPECIALIZED PREDATORY BEHAVIOR OF THE PITCHFORK-MANDIBLED PONERINE ANT *THAUMATOMYRMEX PALUDIS* (HYMENOPTERA: FORMICIDAE)

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ABSTRACT. In this natural history note we describe and illustrate the specialized predatory behavior of the ponerine ant *Thaumatomyrmex paludis* from the Brazilian Amazon. This study of *T. paludis* implies that specialized predation on polyxenid millipedes is widespread in the genus *Thaumatomyrmex*. The observation that one *T. paludis* forager only partly depilated its prey before it started feeding suggests that complete depilation of polyxenids, as reported from *T. contumax*, could be most important when prey items are fed to the larvae, presumably to protect the brood from irritating bristles. Our observations provide an additional example of the sympatric distribution of two *Thaumatomyrmex* species, further supporting the hypothesis that the genus consists of multiple, morphologically similar species.

RESUMO. Neste trabalho descrevemos e ilustramos o comportamento predatório especializado da formiga do grupo Ponerinae *Thaumatomyrmex paludis* da Amazônia brasileira. Este estudo indica que o comportamento predatório especializado em diplópodes da ordem Polyxenida é comum no gênero *Thaumatomyrmex*. Além disso, nossas observações indicam que as formigas forrageiras depilam a presa apenas parcialmente logo após a captura para consumo imediato. Depilação completa da presa, como descrito em *T. contumax*, parece ser mais importante quando a presa é usada para alimentar as larvas, sendo provavelmente praticada para a proteção da cria contra cerdas irritantes. Este estudo ainda demonstra que uma outra espécie do gênero ocorre em simpatria com *T. paludis*. Estas observações corroboram a hipótese de que este gênero é composto por múltiplas espécies morfologicamente similares.

KEY WORDS: predation; ants; sympatry; mandible morphology; Isopoda; Polyxenidae

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INTRODUCTION

The mandibles of an ant are functionally analogous to the hands of a human. They are used to fulfill a variety of tasks such as nest building, defense against enemies, and manipulating brood (Hölldobler and Wilson,

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1990). Most important, the mandibles are precision instruments for catching and handling prey. Ants have evolved diverse predatory behaviors, accompanied by an astounding variety of morphological specializations, including the sickle-shaped mandibles of isopod-hunting *Leptogenys* (Brown, 2000), the filigree forceps-like mandibles of *Martialis heureka* (Rabeling *et al.*, 2008), and the trap jaws of dacetine springtail hunters and of *Odontomachus* ants (Bolton, 2000; Patek *et al.*, 2006). The perhaps most astounding case of mandibular morphological specialization in ants is the bizarre, pitchfork-shaped mandible of the Neotropical ponerine ants in the genus *Thaumatomyrmex*. The genus name, which translates approximately to "wondrous" or "marvelous" ant, emphasizes the outlandish appearance of these remarkable insects (Mayr, 1887).

Since the discovery of the first *Thaumatomyrmex* species no doubt existed that these ants must be specialized predators. Speculations on the most likely prey organisms ranged from snails to termites to the brood of other ant species (Creighton, 1928; Weber, 1942; Kempf, 1975). However, no actual predatory behavior was observed and therefore the nature of the prey and the details about the function of *Thaumatomyrmex*'s mandibles remained a mystery for over a century. Diniz and Brandão (1989) finally solved the puzzle, reporting that *Thaumatomyrmex* ants are specialized predators of bristly millipedes belonging to the family Polyxenidae (Diplopoda: Polixenida: Polyxenidae; *sensu* Condé and Nguyen Duy-Jacquemin, 2008). These first observations were complemented by careful laboratory experiments on *T. contumax* and field observations on *T. atrox* from the Brazilian state of Bahia (Brandão *et al.*, 1991). Additional feeding experiments conducted for *T. contumax* confirmed these results (Delabie *et al.*, 2000; Jahyny *et al.*, 2008).

Polyxenid millipedes represent an unusual prey, because in contrast to heavily sclerotized and chemically well-protected millipede species, polyxenids are soft-bodied and rely on hooked bristles for defense (Eisner *et al.*, 1978). When attacked, they wipe hairs from a pair of bristle tufts at the caudal end of their bodies against the aggressor and when the attacker attempts to clean itself, the barbed hairs lock into the predator's setae, interlink with one another, resulting in the predator's complete immobilization (Eisner *et al.*, 1996). So far, only Neotropical *Thaumatomyrmex* ants and the Indonesian ant species *Probolomyrmex dammermani* are known to be specialized predators of polyxenid millipedes (Brandão *et al.*, 1991; Eisner *et al.*, 1996; Ito, 1998).

Our serendipitous finding of two rarely collected *Thaumatomyrmex* species during field studies in the Brazilian Amazon motivated this short natural history note. It provides information on the predatory behavior of the Amazonian *T. paludis* and an additional example of sympatrically occurring *Thaumatomyrmex* species.

MATERIALS AND METHODS

In the late afternoon of 29 May 2003, a single stray *Thaumatomyrmex* worker was collected at the experimental agricultural field site of the Embrapa, Empresa Brasileira de Pesquisa Agropecuária, in Manaus, Amazonas, Brazil, located at kilometer 28 of Highway AM 010 (2°53′S, 59°59′W; 40–50 m above sea level). The worker was presumably foraging in the thick leaf litter layer of an agroforest, characterized by a diverse mix of fruit and nut trees. *Thaumatomyrmex* colonies are of minute size, sometimes containing fewer than five workers (Brandão *et al.*, 1991; Delabie *et al.*, 2000; Jahyny *et al.*, 2002). Our efforts to locate the colony failed, and we kept the single forager alive in a Petri dish to which we added leaf litter and a moist cotton swab to provide humidity. No food

was added to the formicarium until the start of the feeding experiments on 31 May 2003. For the feeding trials, the ant was transferred into a watchmaker's glass dish and different arthropods such as *Drosophila* flies, isopods, termites, and polyxenid millipedes were added to the arena. Photographs of the foraging worker were taken with a Nikon Coolpix 995, which was handheld to a Wild M-5A stereomicroscope.

In June 2003, we collected a second *T. paludis* worker at the same agroforest site, carrying a polyxenid millipede between its mandibles, presumably returning to the nest. In addition, we collected a single worker of a second *Thaumatomyrmex* species in an adjacent patch of primary terra firme rain forest on 16 April 2003. We were not able to find the colonies of these ants either, and we did not conduct laboratory experiments with these individuals.

To identify the individuals to species level, we used taxonomic keys published by Kempf (1975) and Jahyny *et al.* (2008). Morphometric measurements were taken as defined in Kempf (1975) and are given below. The two workers collected at the agroforest site were identified as *T. paludis* Weber, 1942 (as resurrected from synonymy by Jahyny *et al.*, 2008; see also Longino, 1988) on the basis of the absence of the metanotal suture and the relatively short mandibles (Fig. 1). The morphometric measurements (given in mm) and indices (used as defined in Rabeling *et al.*, 2007) for the two *T. paludis* individuals are: WL (0.97, 1.02), HL (0.65, 0.65), HW (0.63, 0.61), ML (0.61, 0.59), SL (0.57, 0.55), CI (97, 94), SI (88, 85), MI (94, 91). The third *Thaumatomyrmex* individual, collected in a primary rain forest, could not be identified with certainty, but might be related to *T. soesilae* Makhan, 2007 (Fig. 1). However, the taxonomic identity of *T. soesilae* is uncertain, given the inadequacy of the original description and the unavailability of the holotype. The taxonomy of the genus *Thaumatomyrmex* remains utterly confused and is in dire need of a comprehensive revision. Measurements and indices for the second unidentifiable species, hereafter referred to as *T.* sp. Manaus 2, are: WL (0.83), HL (0.55), HW (0.61), ML (0.69), SL (0.47), CI (111), SI (86), MI (125). The specimens were deposited at the Museu de Zoologia da Universidade de São Paulo in Brazil and at the Staatliches Museum für Naturkunde in Karlsruhe, Germany. Individuals were imaged at the Museum of Comparative Zoology using a Leica DFC420 digital camera mounted on a Leica MZ16 dissecting scope. Composite images were assembled using the Leica Application Suite (v. 3.7.0) and Helicon Focus (v. 5.2.9) software packages.

RESULTS

To study and document the predatory behavior of *T. paludis*, we first placed the single worker into the foraging arena and subjected the individual to a cafeteria-style feeding experiment. First, a termite worker was added. The forager antennated the potential prey briefly, turned away, and continued foraging in the arena. Subsequently, a *Drosophila* fly and an isopod were presented to the *Thaumatomyrmex* worker, soliciting the same response: brief antennating followed by disregard. Only the release of a polyxenid millipede into the foraging arena immediately solicited predatory behavior from the *T. paludis* worker, which followed the characteristic pattern described for *T. contumax* (Brandão *et al.*, 1991). The millipede was first antennated by the forager, then briefly secured between the mandibles, stung, and released immediately afterward. The *Thaumatomyrmex* worker retreated and the millipede did not attempt to fling its barbed hairs against the attacker. After the victim was paralyzed, the worker returned,

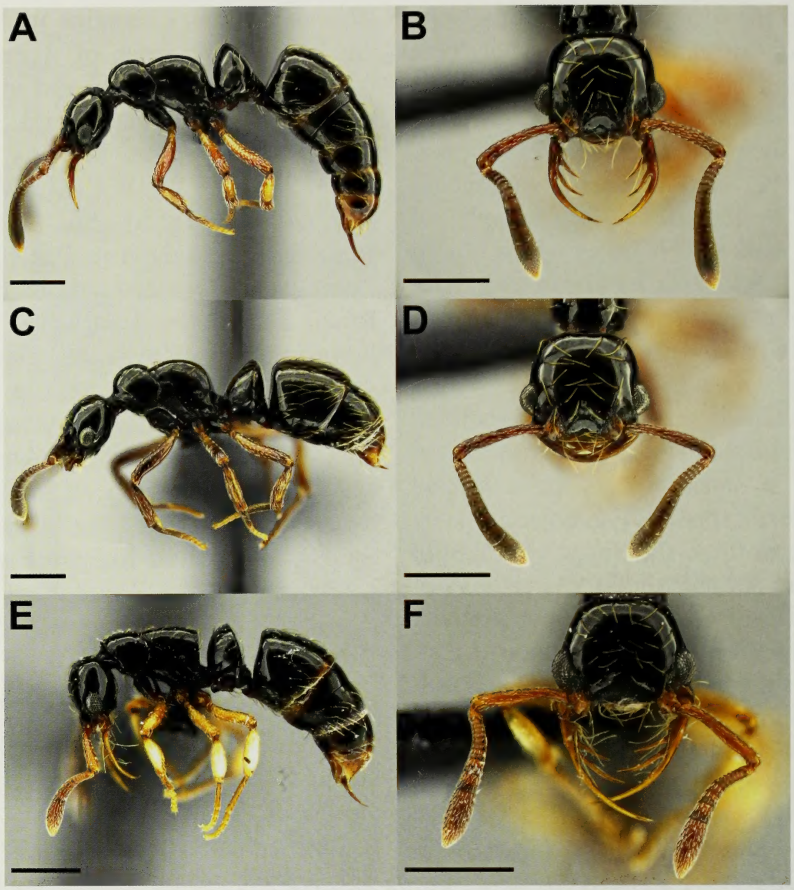

Figure 1. Morphological comparison of *Thaumatomyrmex* individuals collected in Manaus, Brazil. Lateral view of *T. paludis* (A, C) and *T.* sp. Manaus 2 (E) and full face view of *T. paludis* (B, D) and *T.* sp. Manaus 2 (F). The scale bars represent 0.5 mm in all images.

picked up the millipede with its mandibles, holding the armored caudal end of the millipede away from its body, with the ventral side facing toward the ant. Securing the millipede in this position, *Thaumatomyrmex* started brushing the millipede with the stout and thickened setae on its fore tarsi, removing the tufts of setae from the lateral side of the millipede's body close to the head. During the depilation, the ant frequently cleansed its legs, head, and antennae, potentially ridding itself of repellent chemicals contained in the lateral setae. After the removal of a single tuft of setae from one body segment and a second tuft of setae from the opposite side, the *T. paludis* worker started feeding on the ventral side of the millipede (Fig. 2). Interestingly, the polyxenid was not stripped of all its hairs before the ant started feeding (Fig. 2). During the feeding process, the mandibles were frequently removed from the millipede, and then reanchored in the soft tissue of its body, followed by a seesaw movement (Fig. 2), and the ant was licking up exuding hemolymph and tissue particles. Twelve minutes after the *T. paludis* worker first stung its prey, it stopped feeding, picked up the paralyzed

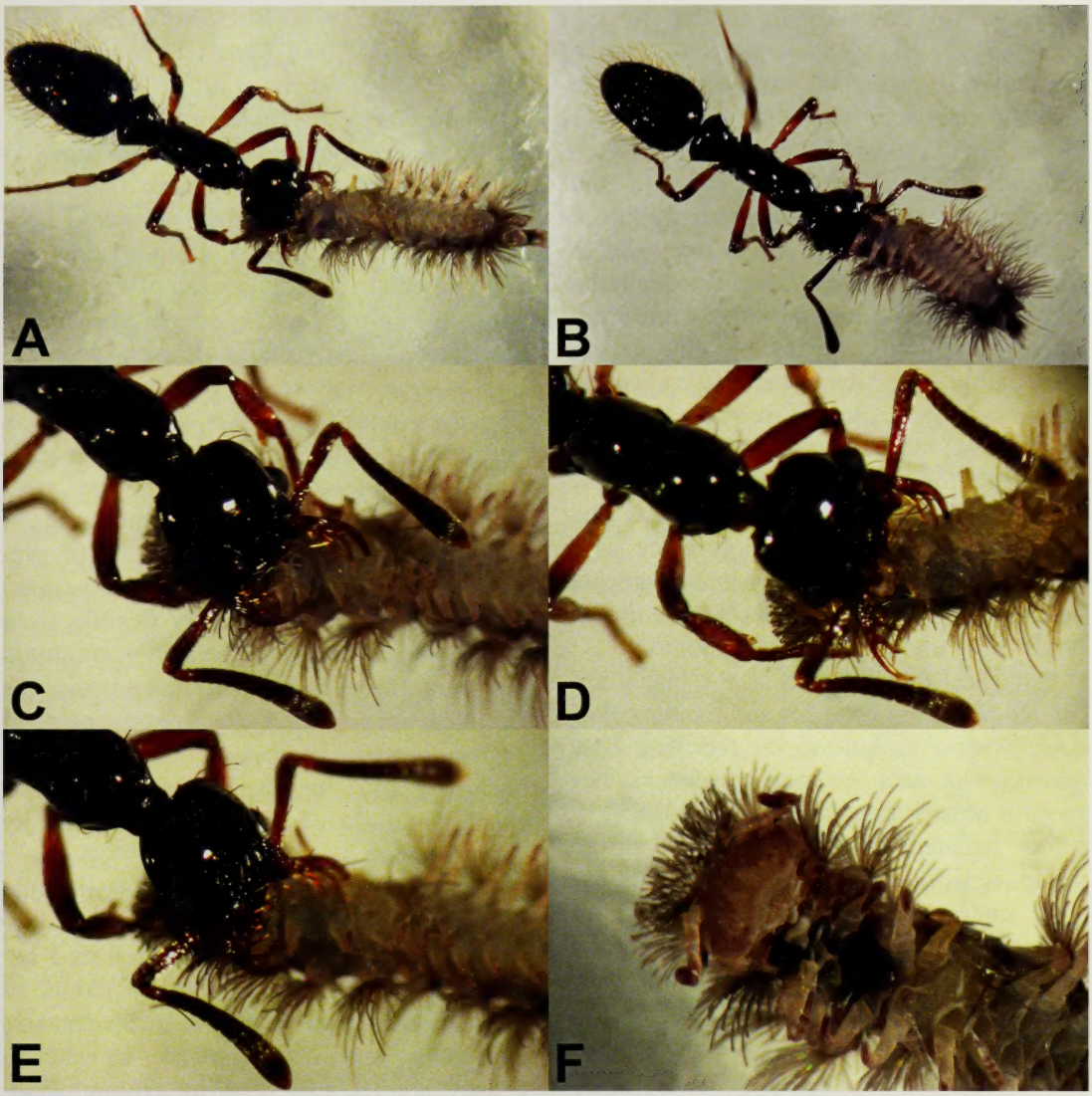

Figure 2. Predatory behavior of *Thaumatomyrmex paludis*. A *T. paludis* worker feeds on a paralyzed and partly depilated polyxenid millipede (A, B). During the feeding, the worker frequently removes its mandibles from the soft millipede and reanchors them in the prey's body, following a seesaw movement (C–E). Ventral view of the polyxenid showing the partial depilation and the feeding marks close to the cephalic region (F).

millipede, and started walking around in the arena, holding the polyxenid head down. Presumably the forager was trying to return to the nest. The ant was monitored for an additional 30 minutes, but no further cleaning or feeding behavior was observed.

DISCUSSION

Our observations show that the Amazonian *T. paludis* preys on polyxenid millipedes, like its congeners *T. contumax* and *T. atrox* (Brandão *et al.*, 1991; Delabie *et al.*, 2000; Jahyny *et al.*, 2008). The behavioral

sequence we observed is similar to that reported for *T. contumax*, consisting of encountering, stinging, stripping, and devouring the prey (Brandão *et al.*, 1991; Delabie *et al.*, 2000; Jahyny *et al.*, 2008). In addition, our observations indicate that foragers may only partly depilate millipedes in the field to feed themselves before returning to the nest. Complete depilation of polyxenids is potentially most important when prey items are fed to the larvae, presumably to protect the soft-bodied immatures from irritating bristles (Brandão *et al.*, 1991). The observation that a second *T. paludis* forager carried a paralyzed polyxenid millipede in the field suggests that specialized predation on polyxenids is a natural behavior exhibited by this species and not merely a behavioral artifact resulting from observation under laboratory conditions.

Ecological factors, such as the highly specialized predatory behavior and minute colony sizes, likely contribute to the fact that *Thaumatomyrmex* ants are rarely observed. Irrespective of their relatively low abundance, the genus radiated into a remarkably diverse group, consisting of 12 described species, plus some undescribed taxa, that are distributed across different biomes in tropical and subtropical Latin America, including Cuba (Kempf, 1975; Baroni Urbani and De Andrade, 2003; Jahyny *et al.*, 2008). Our study provides an additional example of sympatric distribution of at least two *Thaumatomyrmex* species (Brandão *et al.*, 1991; Delabie *et al.*, 2000; Jahyny *et al.*, 2008), further supporting the hypothesis that *Thaumatomyrmex* consists of multiple species, rather than few, morphologically variable species (Longino, 1988). Our collection records of *T. paludis* and *T.* sp. Manaus 2 further demonstrate that *Thaumatomyrmex* is capable of inhabiting a variety of different habitats, ranging from primary rain forests to agroforest sites, consistent with observations on other *Thaumatomyrmex* species (Kempf, 1975; Brandão *et al.*, 1991; Delabie *et al.*, 2000; Baroni Urbani and De Andrade, 2003; Jahyny *et al.*, 2008).

When observing *Thaumatomyrmex* workers preying on polyxenid millipedes, one has to wonder how the ants escape the deadly entanglement of the barbed polyxenid bristles (Eisner *et al.*, 1996). Larger body size and immediate immobilization of the prey by stinging likely prevent workers from being killed by the polyxenid's defense. In addition, it seems noteworthy that the pilosity of *T. paludis* individuals was different in live and point-mounted individuals. In live individuals the long body hairs were erect (Fig. 2), whereas they were appressed in dead individuals (Fig. 1). Cleaning of preserved individuals in water demonstrated that the long hairs were very flexible, even in individuals that had been point mounted for years. It remains to be tested whether the flexible hairs provide a selective advantage to *Thaumatomyrmex* workers by not serving as anchor points for the millipedes' barbed bristles and thereby preventing the deadly entanglement.

Thaumatomyrmex's mandibles beautifully illustrate the degree of extreme morphological specialization to which specialized behavior can lead. The predatory habits of other contemporary species with bizarre mandibles remain unknown and natural history studies still need to explore what, for example, the armadillo ant *Tatuidris* of Mesoamerica (Brown and Kempf, 1967), the bizarre hook-mandibled *Chimaeridris* from tropical Asia (Wilson, 1989), and the Amazonian subterranean predator *M. heureka* (Rabeling *et al.*, 2008) feed on.

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LITERATURE CITED

Baroni Urbani, C., and M. L. De Andrade. 2003. The ant genus *Thaumatomyrmex* in Cuba (Hymenoptera: Formicidae) with description of two new species. *Bulletin de la Société Entomologique Suisse*, **76:** 263–277.

Bolton, B. 2000. The ant tribe Dacetini. *Memoirs of the American Entomological Institute*, **65:** 1–1028.

Brandão, C. R. F., J. L. M. Diniz, and E. M. Tomotake. 1991. *Thaumatomyrmex* strips millipedes for prey: a novel predatory behaviour in ants, and the first case of sympatry in the genus (Hymenoptera: Formicidae). *Insectes Sociaux*, **38:** 335–344.

Brown, W. L. 2000. Diversity of ants. *In* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz eds. *Ants: Standard Methods for Measuring and Monitoring Biodiversity*. Washington, DC, Smithsonian Institution Press.

———, and W. W. Kempf. 1967. *Tatuidris*, a remarkable new genus of Formicidae (Hymenoptera). *Psyche*, **74:** 183–190.

Condé, B., and M. Nguyen Duy-Jacquemin. 2008. Classification actuelle des diplopodes pénicillates (Myriapodes) avec nouvelles définitions des taxa. *Bulletin de la Société zoologique de France*, **133:** 291–302.

Creighton, W. 1928. A new species of *Thaumatomyrmex* from Cuba. *Psyche*, **35:** 162–166.

Delabie, J. H. C., D. Fresneau, and A. Pezon. 2000. Notes on the ecology of *Thaumatomyrmex* spp. (Hymenoptera: Formicidae: Ponerinae) in southeast Bahia, Brazil. *Sociobiology*, **36:** 571–584.

Diniz, J. L. M., and C. R. F. Brandão. 1989. Feeding behavior of *Thaumatomyrmex*. *Notes from Underground*, **2:** 13, Available from: http://www.notesfromunderground.org/archive/oldnotes/nfu2.pdf.

Eisner, T., Alsop, D., Hicks, K., and J. Meinwald. 1978. Defensive secretions of millipeds. *In* S. Bettini (ed.), *Arthropod venoms. Handbuch der Experimentellen Pharmakologie*. Berlin, Springer Verlag.

———, M. Eisner, and M. Deyrup. 1996. Millipede defense: use of detachable bristles to entangle ants. *Proceeding of the National Academy of Sciences of the United States of America*, **93:** 10848–10851.

Hölldobler, B., and E. O. Wilson. 1990. *The Ants*. Cambridge, Massachusetts, Harvard University Press.

Ito, F. 1998. Colony composition and specialized predation on millipedes in the enigmatic ponerine ant genus *Probolomyrmex* (Hymenoptera, Formicidae). *Insectes Sociaux*, **45:** 79–83.

Jahyny, B., J. H. C. Delabie, and D. Fresneau. 2002. Mini-sociétés sans reine chez le genre néotropical *Thaumatomyrmex* Mayr, 1887 (Formicidae: Ponerinae). *Actes des Colloques Insectes Sociaux*, **15:** 33–37.

———, S. Lacau, J. H. C. Delabie, and D. Fresneau. 2008. Le genre *Thaumatomyrmex* Mayr 1887, cryptique et prédateur spécialiste de Diplopoda Penicillata. *In* E. Jiménez, F. Fernández, T. M. Arias, and F. H. Lozano-Zambrano eds., *Sistemática, Biogeografía y Conservación de las Hormigas Cazadoras de Colombia*. Bogotá, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Kempf, W. W. 1975. A revision of the Neotropical ponerine ant genus *Thaumatomyrmex* Mayr (Hymenoptera: Formicidae). *Studia Entomologica*, **18:** 95–126.

Longino, J. T. 1988. Notes on the taxonomy of the neotropical ant genus *Thaumatomyrmex* Mayr (Hymenoptera: Formicidae). *In* J. C. Trager (ed.),

Advances in Myrmecology. Leiden, the Netherlands, E. J. Brill.

MAKHAN, D. 2007. *Thaumatomyrmex soesilae* sp. nov. from Suriname (Hymenoptera: Formicidae). *Calo-derma Supplementary Paper*, **58:** 1–3.

MAYR, G. 1887. Südamerikanische Formiciden. *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien*, **37:** 511–632.

PATEK, S., J. BAIO, B. FISHER, AND A. SUAREZ. 2006. Multifunctionality and mechanical origins: ballistic jaw propulsion in trap-jaw ants. *Proceedings of the National Academy of Sciences of the United States of America*, **103:** 12787–12792.

RABELING, C., J. M. BROWN, AND M. VERHAAGH. 2008. Newly discovered sister lineage sheds light on early ant evolution. *Proceedings of the National Academy of Sciences of the United States of America*, **105:** 14913–14917.

———, S. P. COVER, R. A. JOHNSON, AND U. G. MUELLER. 2007. A review of the North American species of the fungus-gardening ant genus *Trachymyrmex* (Hymenoptera: Formicidae). *Zootaxa*, **1664:** 1–53.

WEBER, N. A. 1942. The genus *Thaumatomyrmex* Mayr with description of a Venezuelan species (Hym.: Formicidae). *Boletin de Entomologia Venezolana*, **1:** 65–71.

WILSON, E. O. 1989. *Chimaeridris*, a new genus of hook-mandibled myrmicine ants from tropical Asia (Hymenoptera: Formicidae). *Insectes Sociaux*, **36:** 62–69.